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Current Biology

Australia's recently established predators restore complexity to food webs simplified by extinction

Highlights

- Australia's fauna has been radically reorganized since the Late Pleistocene
- New predators share little functional overlap with extinct predators
- Yet, current-day food webs have been rewired in resemblance to the Late Pleistocene
- Prehistory provides important perspectives to current-day conservation

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In brief

Investigating how the biotic reorganization of Australia's predator community has shaped the form and function of food webs, Wooster et al. unveil that, despite having distinct traits, recently established predators rewire food webs in the image of the Late Pleistocene. However, food web similarities are dependent on apex predator protection.

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Australia's recently established predators restore complexity to food webs simplified by extinction

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SUMMARY

Since prehistory, humans have altered the composition of ecosystems by causing extinctions and introducing species. However, our understanding of how waves of species extinctions and introductions influence the structure and function of ecological networks through time remains piecemeal. Here, focusing on Australia, which has experienced many extinctions and introductions since the Late Pleistocene, we compared the functional trait composition of Late Pleistocene (130,00–115,000 years before present [ybp]), Holocene (11,700–3,000 ybp), and current Australian mammalian predator assemblages (≥70% vertebrate meat consumption; ≥1 kg adult body mass). We then constructed food webs for each period based on estimated prey body mass preferences. We found that introduced predators are functionally distinct from extinct Australian predators, but they rewire food webs toward a state that closely resembles the Late Pleistocene, prior to the megafauna extinctions. Both Late Pleistocene and current-day food webs consist of an apex predator and three smaller predators. This leads to food web networks with a similar total number of links, link densities, and compartmentalizations. However, this similarity depends on the presence of dingoes: in their absence, food webs become simplified and reminiscent of those following the Late Pleistocene extinctions. Our results suggest that recently established predators, even those implicated in species extinctions and declines, can restore complexity to food webs simplified by extinction.

INTRODUCTION

Prehistoric and ongoing human-driven extinctions of large animals are understood to have driven global declines in interaction network complexity,[1–3] particularly through the removal of top-down trophic interactions in ecosystems.[4] Conversely the movement of animal species across the globe, facilitated and accelerated by humans, has created a suite of new ecological networks characterized by novel interactions.[5,6] Introduced species can have profound influences on their recipient ecosystems, particularly mammalian predators,[7] which have been implicated in the decline and extinction of native prey.[8] Yet, simultaneously, introduced species can also restore ecological functions and complexity that were lost following extinctions.[9,10] The extent to which predator introductions may replace lost ecological functions and rewire interaction networks remains unknown.[6,11]

Australia's predator assemblage and broader mammalian communities have experienced high extinction rates since human arrival (estimated ~65,000 years before present [ybp][12]). By ~45,000 ybp, Australia had lost all but one of its herbivorous megafauna ≥44 kg (22 species[13]) as well as its largest mammalian predator, the 110-kg marsupial lion (*Thylacoleo carnifex*). During the mid-Holocene, dingoes (*Canis*

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Figure 1. Australia's mammalian predator community has been radically reorganized by extinction and introduction since the Late Pleistocene

Current-day mammalian food webs feature just a single predator also present in the Late Pleistocene (see Table S1). Top panel pictures the predator community (≥70% vertebrate meat consumption; ≥1 kg adult body mass) present in Australia during the Late Pleistocene. Late Pleistocene predators, clockwise, are the Tasmanian devil, marsupial lion, thylacine, and tiger quoll. Bottom panel pictures the current-day predator community. Current-day predators, clockwise, are red fox, cat, dingo, and tiger quoll. Illustrations by O.S.

dingo, 15–25 kg[14]) established across Australia (likely somewhere between 8,000 and 3,500 ybp), which may have occurred with or without human assistance.[15] Around this time, thylacines (*Thylacinus cynocephalus*) and Tasmanian devils (*Sarcophilus harrisii*) went extinct on the mainland (~3,000 ybp), potentially due to predation or competition with dingoes.[16] The 1–5 kg tiger quoll (*Dasyurus maculatus*) is the largest remaining mammalian predator present in both Late Pleistocene and current food webs. However, two more predators were added to Australia's assemblage by European colonists: cats (*Felis catus*) were introduced in ~1788[17] and red foxes (*Vulpes vulpes*) were introduced in 1871.[18] At the same time, Europeans began killing dingoes on the mainland and thylacines in Tasmania to reduce threats to livestock[19] and began widespread land clearing and habitat destruction. An extinction wave followed, primarily affecting small- to medium-sized mammals (35–5,500 g[20]). Since European colonization, Australia has lost a total of 40 mammals to extinction and a further 57 are threatened with extinction.[21,22] Foxes and cats are implicated in many of these declines and extinctions through predation, which is intensified by the removal of Indigenous people and their land management practices,[21] widespread habitat destruction, and mesopredator release following dingo persecution.[23,24]

Predators play important roles in ecosystems by influencing herbivore population sizes and behaviors, as well as smaller predators and thus their prey.[25] In doing so, predators shape energy and nutrient flows through food webs, primary productivity, habitat structure, and the abundance and diversity of lower trophic levels.[4] Predator traits determine how these interactions are realized by shaping prey preferences, habitat usage, and so on.[26,27] Food webs allow for the quantification and analysis of these fundamental ecological interactions,[28] providing a framework for understanding how ecological change can influence ecological communities.[2,3,29] As such, understanding how the structure of contemporary mammalian communities compares to those of the past would bring a novel perspective to ongoing debates on conservation and management in Australia and beyond.

Here, we analyzed how extinctions and introductions have influenced the functional traits of Australia's non-human mammalian hypercarnivorous predator assemblage (≥70% vertebrate meat consumption; ≥1 kg adult body mass) and the structure of food webs. We specifically evaluated predator ecological functions and food webs for four time periods that reflect changes in Australia's predator assemblage: a period of the Late Pleistocene (~130,000–115,000 ybp), early Holocene (~11,700 ybp), mid-Holocene (~3,000 ybp), and current day (Figure 1). We investigated three aspects of ecological change: (1) how extinctions and introductions have shaped the functional trait structure of Australian predator assemblages, (2) how Holocene-established predators have reshaped continental-level food webs (average of Australian biomes), and (3) each predator's role within the food webs. Across each of these questions, we investigated the implications of dingo extirpation, which is attempted across much of Australia.[14,30] In doing so, we present a unique perspective of Australian ecological dynamics by incorporating a prehistoric perspective of ecological change and bring forth new understandings of the macroecological consequences of apex predator extirpation.

RESULTS

Functional trait composition of Australia's predator assemblage

We began by analyzing the functional trait composition of Australian predator assemblages for each of the four periods. We focused on hypercarnivorous mammals (≥70% vertebrate meat consumption) with an average adult body mass ≥1 kg, for which we compiled seven traits that influence predator-prey dynamics. These included: body mass, maximum prey size, hunting modes (pursuit/pounce-pursuit/ambush), locomotion (cursorial/scansorial/generalized), hunting group size, bite force, and fecundity (see Table S5). We then constructed functional trait spaces to synthetically describe how predators differ from each other in terms of their traits, thus allowing

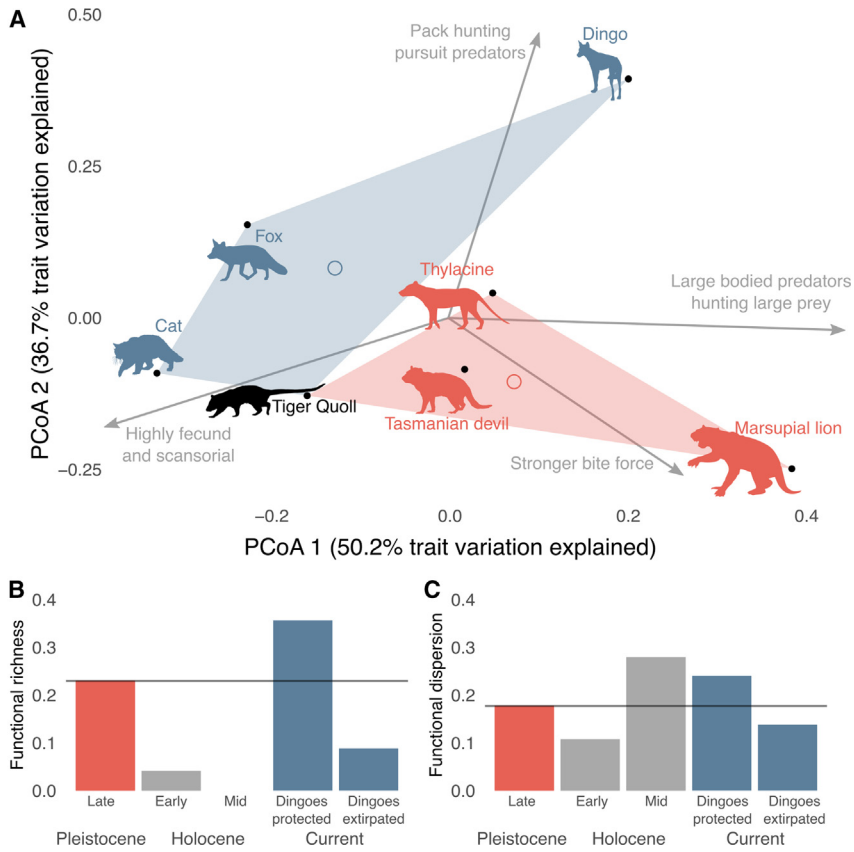

Figure 2. Shifts in Australian predator functional trait space following extinctions and recent establishments

(A) Predator functional trait space for mammalian predators that have occurred on mainland Australia in the past ~130,000 years (see also Table S2). Silhouettes of extinct predators are red, extant-native are black, and recently established predators are blue. Distances between species reflect pairwise dissimilarity in trait compositions. Convex hulls are shown for the Late Pleistocene community (red polygon) and for the current-day community (blue polygon). Open circles indicate community centroids.

(B and C) (B) Functional richness and (C) functional dispersion for each time period. Horizontal lines indicate Late Pleistocene functional measures for comparison with other time periods.

comparisons between each time period. To summarize changes in mammalian predator functional traits, we calculated two functional diversity measures for each time period: *functional richness* and *functional dispersion*. These describe overall trait diversity and the average trait dissimilarity between species, respectively.

We found that the Late Pleistocene extinction of the marsupial lion, the largest mammalian predator of the time, caused an 83% decline in predator *functional richness* and 40% decline in *functional dispersion* (Figures 2B and 2C). These declines were further exacerbated by the mid-Holocene mainland extinctions of the Tasmanian devil and thylacine, which led to the lowest functional richness of any time period. It has been argued that the latter extinctions were driven by the arrival of dingoes.[16]

These prehistoric and historic losses were counteracted by the establishment of dingoes, foxes, and cats, which increased functional diversity. These changes are, however, influenced by whether dingoes are present or extirpated. Where dingoes are present, functional richness and dispersion are 55% and 35% greater than in the Late Pleistocene, respectively. The removal of dingoes from current-day Australian ecosystems results in a functional richness and dispersion decrease of 75% and 43%, respectively.

The resulting trait space, where dingoes are present, is similar to that of the Late Pleistocene in total functional richness (e.g., functional space area, Figure 2A) but has no overlap in functional space due to the distinct traits of foxes, cats, and dingoes. This suggests that recently established predators are functionally novel in Australia. Foxes and cats occupy distinct regions of functional trait space compared with Late Pleistocene predators (Figure 2A), driven by their smaller body masses, smaller maximum prey sizes, and higher fecundities. Likewise, dingoes are functionally novel to Late Pleistocene species as they are a relatively small-bodied, pack-hunting predator with a large maximum prey size. The arrival of dingoes and their novel prey-size range may explain the mainland extinction of both Tasmanian devils and thylacines through both intraguild predation and competition. Functional dispersion was most similar between the mid-Holocene and current-day predator communities (Figure 2C).

Prey body mass ranges of Australia's predators

We estimated prey body mass preferences for each predator. These estimates indicated that dingoes are capable of hunting large-bodied megafauna, though to a lesser extent than the marsupial lion (Figure 3), and that recently established mesopredators are likely to collectively rely on smaller-bodied prey species more than did extinct and extant native predators. We acknowledge, however, that realized predation pressure is more complex than preferred prey size and is likely driven by wider ecological context, such as the presence of larger predators and complex intraguild interactions. Indeed, empirical evidence suggests that dingoes can suppress both foxes and cats,[23] that foxes suppress cats,[31,32] and that these top-down pressures can shape the effects of these predators on their prey.[23]

Rewiring of Australia's mammalian food webs

To understand how differences in prey body mass preferences influenced potential food web structures, we constructed mammalian interaction networks between Australian predators and potential prey for each time period. These networks accounted for both extinctions and introductions of prey species, including extinct Late Pleistocene megafauna and current introduced species. We then analyzed the structures of these networks in terms of a suite of network metrics that we synthesized with a principal coordinates analysis. These metrics were

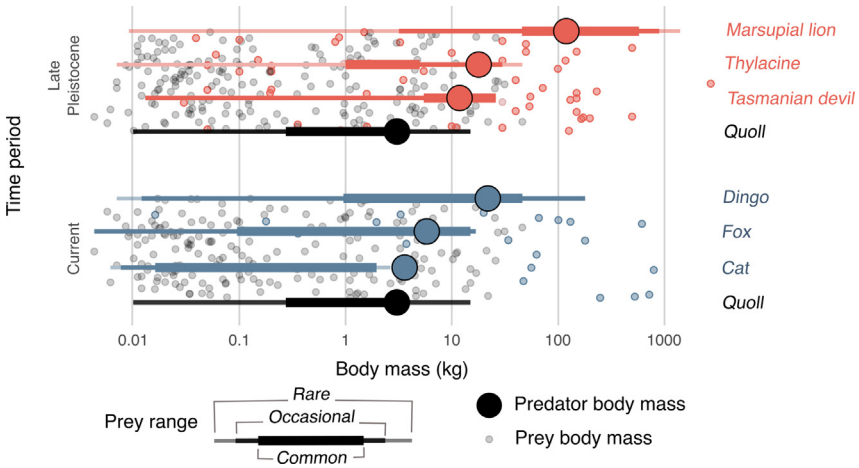

Figure 3. Potential prey body mass ranges of Australian mammalian predators

Body masses are shown for extinct (red), extant-native (black), and recently established (blue) predators (larger circles) and prey species (smaller circles) that occurred on mainland Australia in the Late Pleistocene and the current day. Body mass ranges for commonly, occasionally, and rarely consumed prey species for each predator are indicated by varying line thickness. Vertical gray lines indicate break points for prey body mass categories. Current-day prey include introduced species.

connectance, total number of interactions, link density, compartmentalization, total system throughput, average compartment throughflow, link weight, number of compartments and the effective connectance, effective flows, effective nodes, and effective roles of networks (see Table S6).

We found that Late Pleistocene and Holocene extinctions of predators and megafauna simplified mammalian interaction networks by reducing the number of predator and prey species and their interactions (Figure S4). These simplifications were offset by recently established predators and introduced prey, which increased the number of links and link density and reduced network compartmentalization (Figure S4). These changes led to a marked resemblance between current and Late Pleistocene food web metrics (Figure 4).

However, this resemblance is contingent upon the presence of dingoes. The removal of dingoes reduces current network structural resemblance to Late Pleistocene interaction networks (Figure 4). On average, dingo extirpation reduces the number of food web links by 29%, which is comparable with the 32% of links lost with the extinction of *Thylacoleo*. These simulations indicate that the loss of dingoes, Australia's sole mammalian apex predator, leaves large- and medium-bodied herbivores and mesopredators without predators and can thus potentially increase predation pressure on smaller herbivores.

Predator roles in Australian food webs

We then used the same interaction networks analyzed above to assess predator roles in interaction networks by calculating metrics that describe each predators' location in each network (i.e., eigenvector, degree, closeness, and betweenness centrality). We found that the ecological roles of dingoes likely sit somewhere between the thylacine and marsupial lion. The similarity between dingoes and the marsupial lion is driven by their large mean prey sizes and eigenvector centrality, whereas dingoes and thylacines are similar in their numbers of consumers and resources and degree centrality (Figure 5). Finally, tiger quolls, the only mammalian predator remaining from the Late Pleistocene, have shifted their ecological roles within current-day networks compared with those of the Late Pleistocene. This is driven by their higher betweenness and closeness centrality in current networks.

DISCUSSION

Our results suggest that the establishment of functionally novel predators can rewire food webs simplified by extinction. By comparing current-day Australian mammalian food webs with prehistoric ones, we show that food webs today are remarkably similar in topology to those of the Late Pleistocene, despite strong differences in predator trait compositions (Figure 2). This is largely driven by the ecological uniqueness of dingoes as social hunters that, relative to their body mass, can hunt large prey and establish strong top-down forces on mesopredators. The extirpation of dingoes can shift ecological mammalian interaction networks by altering the network roles of smaller predators (Figure 5). Our estimated networks show that current-day food webs without dingoes resemble those of the Early Holocene, simplified by the extinction of an apex predator.

Present-day and Late Pleistocene mammalian interaction networks both possess an apex predator capable of hunting large prey, alongside three predators hunting smaller prey. As inferred through their similar position in food webs and their prey size, the top-down pressures from dingoes may have some similarity to those from marsupial lions in Late Pleistocene ecosystems, despite diverging in important traits such as body mass, hunting style, and bite force. Whereas marsupial lions hunted now-extinct megafauna, protected dingo packs have the capacity to hunt and place top-down pressures on introduced megafauna such as feral pigs (*Sus scrofa*), horses (*Equus caballus*), and Sambar deer (*Rusa unicolor*).[33,34] The top-down pressures dingoes exert on megafauna are, however, dependent on robust packs that hunt larger megafauna and drive behaviorally mediated trophic cascades through socially learned hunting behavior.[25,35]

We also note that as much as the largest Late Pleistocene megafauna, *Diprotodon optatum* (2,700 kg), were likely too large to be hunted by marsupial lions, introduced camels (*Camelus dromedarius*) and buffalo (*Bubalus bubalis*) are also larger than the largest prey estimated for dingoes, although dingoes have been observed hunting sub-adult buffalo.[33] This reflects long-term patterns in mammalian assembly, where adults of the largest megafauna species are relatively immune to predation and thus bottom-up regulated by resource availability, as is visible in the fossil record and in modern African megafauna communities.[36,37]

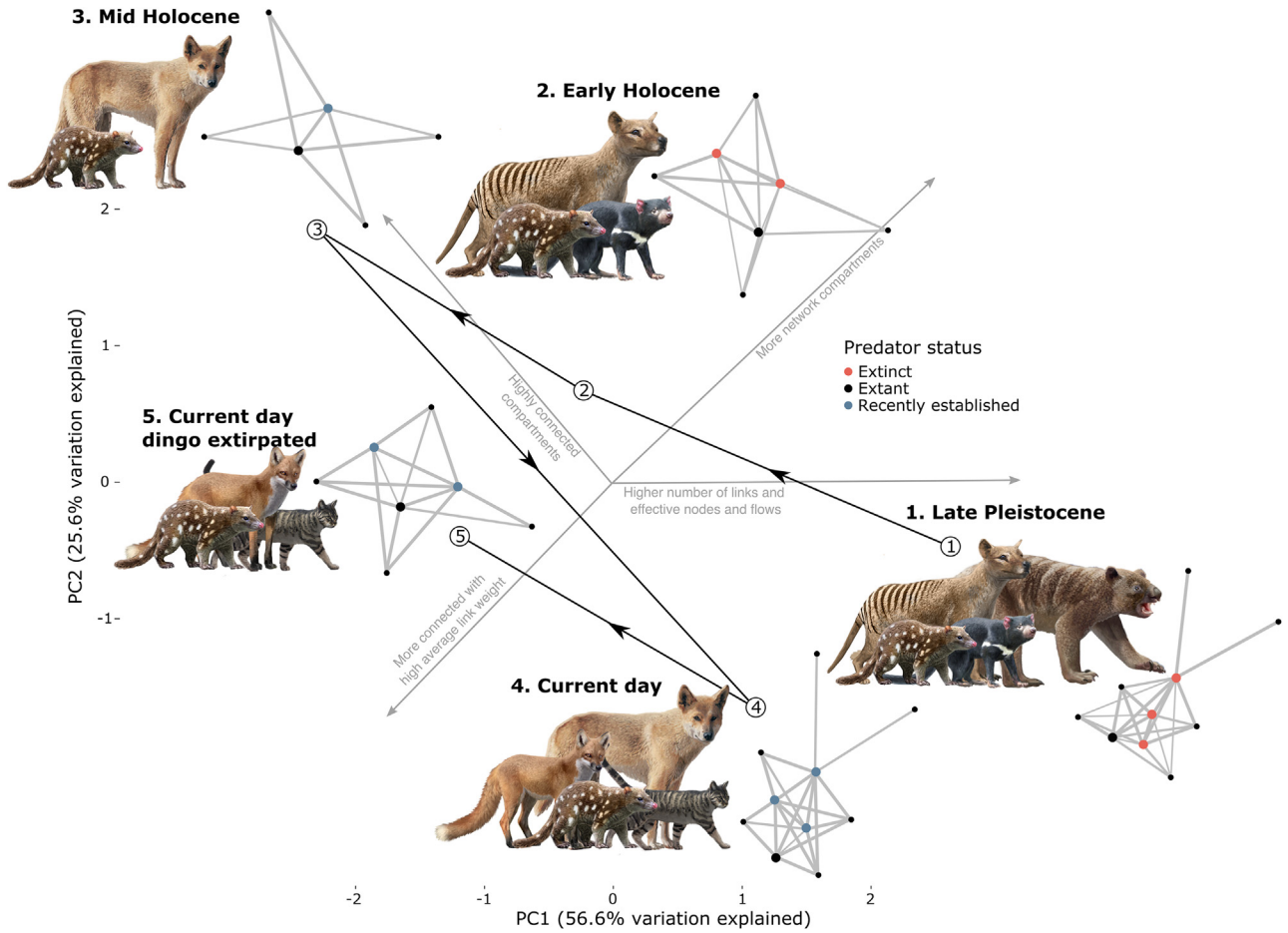

Figure 4. Recently established predators restore complexity to Australian food webs

Average trajectory of change to food web structures across time periods and following dingo extirpation (for biome-level interaction networks, see Figures S3 and S4). The first two principal components explained 82.2% variance. Inset networks are simplified food webs with links between predator (larger nodes) and prey (smaller nodes) categories and between predators. They represent the average network across mainland Australia. The thickness and darkness of the line indicates the interaction strength, with thicker lines indicating a higher interaction strength. Inset square shows principal-component analysis (PCA) loadings with network structure metrics (see Table S3). Visualized food webs presented feature prey species pooled into the following categories: <100 g, 100 g–1 kg, 10–50 kg, 50–100 kg, 100–1,000 kg, and >1,000 kg—analyzed food webs are not pooled into these categories. Illustrations by O.S.

Additionally, our work highlights that the ecological roles of even native predators within food webs can shift with introductions and extinctions. We found that the network position of quolls within each time period was dependent on the predators and prey present. Within Late Pleistocene food webs, quolls were not central to Australian food webs. Yet, in current-day food webs, quolls are more central, with higher betweenness and closeness centrality than both foxes and cats. Quolls become even more central when dingoes are absent, which pushes quolls further from their predatory roles during the Late Pleistocene. Our results thus suggest that even historic native predators can take up novel positions within food webs as the pool of co-occurring species changes.

The smaller body masses of recently established predators are likely to drive novel predation pressures within present-day mammalian interaction networks, with our results estimating that smaller prey may experience increased predatory interactions due to recently established predators' preferences for smaller prey. Yet, empirical work has found that dingoes benefit native mammals by suppressing fox and cat populations[24] and altering their behavior.[38,39] Taken together with our results, the loss of dingoes from ecosystems may drive intensified predation pressure on small mammals and result in the simplification of food webs.

Whereas our work deals in the binary of dingo extirpation or protection, there is a third state that, despite being commonplace across Australia, is challenging to quantify—dingo persecution. The persecution of dingoes can lead to the loss of pack hunting and thus reduced prey sizes, which likely alters how they influence mesopredators and herbivores.[23] Some ecologists have theorized that the loss of pack hunting from dingo populations might result in a trophic downgrading of the species[40]; however, insufficient evidence exists for us to draw any conclusions on how dingo persecution shapes Australian food webs. Our work is consistent with previous research[14,41] that suggests that the high predation pressure that small animals can face from foxes and cats is at least partially interconnected with long-term and widespread dingo persecution[38] and

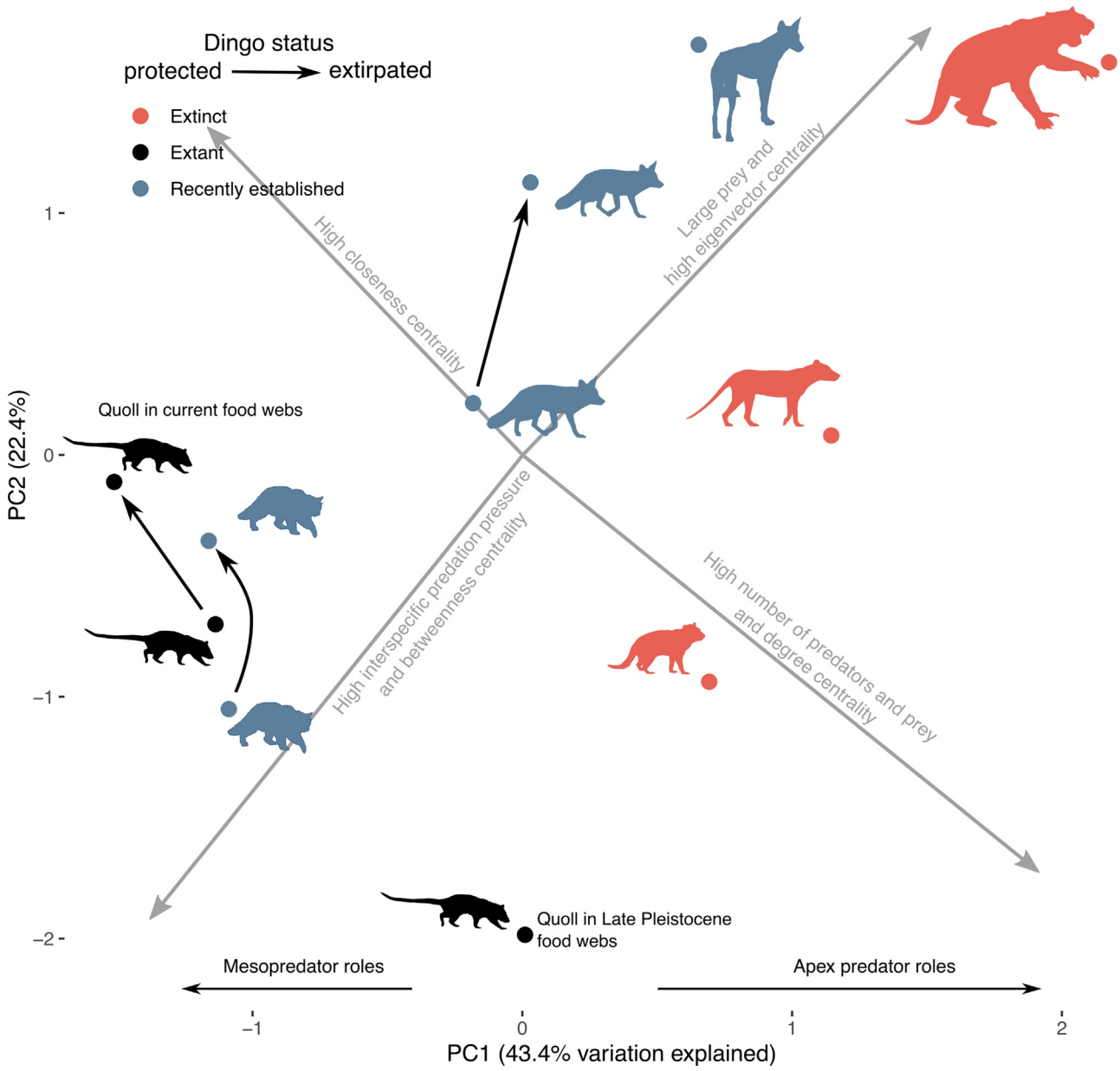

Figure 5. Dingo extirpation shifts food webs further from those of the Late Pleistocene

We used metrics of centrality that describe a species' relative influence on the food web, with higher values indicating that a species is more connected to the overall food web (see Table S4). The position of extinct predators (red), extant-native (black), and recently established (blue) predators indicate their average ecological role across biome-level food webs. The quoll is represented across its Late Pleistocene, current day, and current-day dingo extirpated predatory role. Arrows show the transition of ecological roles of predators in current-day food webs when dingoes are extirpated from ecosystems.

habitat change,[21,42] which interact and amplify the extinction risk.[42,43]

We present a broad comparison of prehistoric to contemporary ecological dynamics among mammalian predators and prey. Though our analyses drew from the best available data, uncertainty remains. Anecdotal evidence of thylacine diets is limited to Tasmania, where thylacines were larger-bodied than their mainland relatives,[44] potentially leading to overestimates of their prey size in this analysis. Further, although we only focus on mammalian predators, extinct and extant reptilian predators were and are important in their respective ecological networks.[45,46] However, excluding them was deemed appropriate as reptilian predators are not ecologically similar to mammalian predators because of lower per capita metabolic rates and therefore less frequent and less active hunting.[47] Likewise, our results did not consider humans as predators, given that human hunting capacities are culturally dynamic, with high variance between different Indigenous groups and between Indigenous groups and European colonists.[48] Detailed work from the Western Deserts of Australia has demonstrated the profound

influence of Indigenous people on past and contemporary food webs.[49] Future research, in collaboration with Indigenous communities and archaeologists, may improve our ability to account for people as members of ecological communities on macroecological scales.[50]

Additionally, our analysis does not capture finer-scale spatial variation in food webs. Although our biome-level results based on reconstructed distributions for extinct species showed similar results (Figure S3), these reconstructions are prone to error, especially in arid landscapes like central Australia. Although not possible with extinct species, future work could look to quantify Australian food webs on landscape scales by assessing how the loss of dingoes shapes food web properties and linking these changes with ecosystem function, extending our macroecological results to more local scales. This could be done with both explicit dietary information[51] and through a similar trait-based inference method.[52] Our work also highlights the fact that similar network topology does not always infer similar functioning within networks. We found marked similarities between the Late Pleistocene and current-day networks, despite major differences in the functional trait composition and predators playing distinct and novel ecological roles within the networks. This suggests that, while similar in topology, current-day food webs may function differently to their prehistoric counterparts. Finally, it is important to note that the data and methods used in this study cannot infer how the rewiring of these food webs has shaped ecosystem functionality or stability, leaving these as important future avenues of study.

Prehistory provides important ecological and evolutionary context that can help us understand novel community assemblages and food webs.[53] By looking to prehistoric extinctions and recent establishments, we show that recently established mammals in Australia can rewire food webs with network properties that resemble those prior to extinctions, but only when dingoes are present in the system. These findings further bolster the case for the ecological importance of apex predators in structuring ecosystems from the top down.[1,54]

RESOURCE AVAILABILITY

Lead contact

Further information and requests should be directed and will be fulfilled by the lead contact, Eamonn Wooster (eif.wooster@gmail.com).

Materials availability

The study did not generate new unique reagents.

Data and code availability

All data reported in this paper have been deposited at Zenodo and are publicly available. DOIs are listed in the key resources table.

All original code has been deposited at Zenodo and is publicly available. DOIs are listed in the key resources table.

Any additional information required to reanalyze the data reported in this paper is available from the lead author upon request.

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AUTHOR CONTRIBUTIONS

O.S.M., E.J.L., and E.I.F.W. led the conception of the manuscript and data collection. O.S.M., E.J.L., and E.I.F.W. led the analyses. O.S.M. wrote the first manuscript draft. O.S.M., E.J.L., A.D.W., E.I.F.W., J.P.W.S., and C.J.S. contributed equally to developing the manuscript. E.I.F.W. and E.J.L. led revisions to the manuscript. All other authors contributed equally to revising manuscript drafts. O.S. illustrated the figures.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Australian predator assemblage functional traits
  - Estimating prey ranges for predators
  - Constructing Australian food webs
  - Analyzing food web structures and predator roles

SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data collated from online resources	Zenodo	https://zenodo.org/records/13755842
Software and algorithms		
R Statistical Software	R Project	https://www.r-project.org/
Contributed R packages	Comprehensive R Archive Network (CRAN)	https://cran.r-project.org/
R code	Zenodo	https://zenodo.org/records/13755842

METHOD DETAILS

Collating Australian mammal communities

We constructed species lists of mammals for mainland Australia that reflect: (i) before Late Pleistocene extinctions (~130,000 – 115,000 ybp); (ii) after Late Pleistocene extinctions before dingo arrival (~11,700 ybp; 'early Holocene'); (iii) after dingo colonisation and mainland Tasmanian devil and thylacine extinction (~3,000 ybp; 'mid-Holocene'); (iv) current-day after fox and cat colonisation. We used the PHYLACINE database[55] to identify all Australian mammals present before the Late Pleistocene extinctions, those that went extinct during the Late Pleistocene, and those that went extinct after European arrival. All Australian mammals that occurred at least during the Late Pleistocene were identified using 'present-natural range' maps in PHYLACINE which are suitable proxies for mammal ranges during the last interglacial (130,000 – 115,000 ybp) as they are estimates of mammal ranges under current climate conditions under a counterfactual scenario where species ranges had not been affected by humans. While we acknowledge that these distributions are coarse estimates based on co-occurrence records, they represent the best available means to evaluate how extinctions have shaped current biodiversity. We used 'current' maps from PHYLACINE to identify the distributions of mammals today, which are based on IUCN Redlist distributions.[55] Maps derived from Wallach et al.,[56] were used to identify Holocene-established mammals.

We selected medium-large mammals (>1 kg) that are hypercarnivorous (≥70% vertebrate meat) as predators (traits from PHYLACINE). We identified five marsupial predators: marsupial lions, thylacines, tiger quolls and Tasmanian devils. A giant rat-kangaroo may have been hypercarnivorous, but as little is known of its ecology, we excluded it from our analyses. We identified three Holocene-established predators: dingoes, red foxes, and cats (See Table S1). We excluded humans from all analysis as they have distinct ecological impacts that are not comparable to non-human predators and are culturally dynamic.[57,58]

QUANTIFICATION AND STATISTICAL ANALYSIS

Australian predator assemblage functional traits

We collated seven functional traits for each predator (See Table S5), including body mass, maximum prey size, hunting modes (pursuit/pounce-pursuit/ambush), locomotion (cursorial/scansorial/generalised), hunting group size (solitary/flexible/social), bite force, and fecundity ([litter size × litters per year] / reproductive group size). We gathered traits from *CarniTraits*[59] and peer-reviewed literature. We then calculated pairwise Gower's distances between each predator. Gower distance allows for the weighting of traits, which we weighted equally. To weight categorical traits (e.g. locomotion), which we coded as separate binary traits for each categorical level, we weighted these by a proportion of the number of categories (e.g. cursorial/scansorial/generalized each weighted by 1/3).[10] A principal coordinate analysis was performed on the Gower distance matrix with a Cailliez correction to correct for negative eigenvalues.[60] We used the '*envfit*' function in the R package '*vegan*'[61] to identify traits structuring the first two axes (Table S2) using squared correlation coefficients (r^2).

Two functional diversity metrics were calculated for each predator assemblage in each time period using the "dbFD" function in the 'FD' package.[60] Functional richness describes the total volume of the functional trait space present and varies between 0 and 1 [62] Functional richness cannot be calculated for less than three species. Functional dispersion describes average species dissimilarity, calculated as the average distance of each predator from the assemblage centroid.[62] Functional dispersion has no upper limit.

Estimating prey ranges for predators

We identified the best evidence for each predator's diet to estimate interactions with prey. For extant predators, we extracted quantitative diet studies in Australia from CarniDIET,[63] including red foxes (diet studies $n = 26$), tiger quolls ($n = 9$), and Tasmanian devils ($n = 3$). Dingo ($n = 33$) and cat ($n = 14$) diet studies were not available from CarniDIET and were therefore collated via targeted literature searches across Google Scholar and Web of Science (See Figure S1). For thylacines, we used anecdotal observations of prey

interactions and suggested prey from functional morphology studies. For marsupial lions, we extracted diet studies from CarniDIET for potential diet proxies, including tigers, (*Panthera tigris*; $n = 26$), lions (*P. leo*; $n = 21$), and jaguars (*P. onca*; $n = 17$) (See Figure S2). Extant felid diets were considered suitable proxies for marsupial lions if their common prey range included the body mass range of *Sthenurus* spp. (72-173 kg) which were likely common prey for marsupial lions.[64]

Prey species were defined as 'common' when occurring in $\geq$20% of a predators diet, 'occasional' between 5% and 20%, and 'rare' in <5%. If prey were not described at the species-level, we took a conservative approach by dividing the frequency of occurrence of the prey item by the number of species that the prey item could refer to in the area and the median body mass used. For thylacines, we assigned common prey from 1–5 kg occasional prey from 5–30 kg and rare prey up to 46 kg.[65,66] For marsupial lions, both tiger and lion common prey were comparable and included *Sthenurus* body mass range (Figure S2B). However, we used lions as the proxy for marsupial lions as they best captured the prey range including *Sthenurus* prey body mass range and an occasional reliance on smaller macropods.[67]

Constructing Australian food webs

We identified all potential predation links between predators and prey that co-occurred for each time period in each Australian biome. Biomes included: Tropical & Subtropical Moist Broadleaf Forests; Temperate Broadleaf & Mixed Forests; Tropical and Subtropical Grasslands, Savannas and Shrublands; Temperate Grasslands, Savannas and Shrublands; Montane Grasslands and Shrublands; Mediterranean Forests, Woodlands and Scrub and; Deserts and Xeric shrublands and were extracted from Olson et al.[68] Each prey species had its dietary importance assigned to each predator, depending on the body mass range of predator's common (strength = 3), occasional (strength = 2) and rare (strength = 1) prey. These were interpreted as potential interaction strengths.

We removed intraspecific links and all links from smaller to larger predators to reflect the fact that smaller predators rarely place top-down pressures on larger ones. Intraguild interactions were added from thylacine to tiger quolls and Tasmanian devils, foxes to tiger quolls and cats, and weak interactions added between tiger quolls and cats in both directions and for Tasmanian devils and tiger quolls in a single direction.

We used the '*igraph*' package[69] to create food web networks based on estimated interactions between predator and prey species for each time period and for each biome. Each adjacency matrix of predator-prey interactions were converted into food webs as a directed unipartite network with the '*igraph*' package.[69]

Analyzing food web structures and predator roles

To analyze changes in network properties, we calculated a suite of metrics using the '*omnivor*'[70] and '*NetIndices*'[71] packages. These metrics were connectance, total number of interactions, link density, compartmentalization, total system throughput, average compartment throughflow, link weight, number of compartments and the effective connectance, effective flows, effective nodes, and effective roles of networks. These are all metrics commonly used in ecological networks analysis.[28,72,73] Comprehensive overviews of some of these metrics are available,[72,74] one of which, Tylianakis et al.[74] states that "....*conservation of complex emergent properties such as network stability will likely require monitoring of a suite of metrics*", which influenced our decision to incorporate multiple network metrics in descriptions of network structural change (See Table S6).

To synthesize changes in these metrics across the four time periods, we used a principal components analysis with the '*prcomp*' function. The raw data for this was at the biome level. However, to simplify visualization, we present the average across biomes for the main text figures (see Figure S3 for biome-explicit results). We visualized food webs by pooling prey species into the following categories: <100g, 100g– 1kg, 10kg – 50kg, 50kg – 100kg, 100 – 1000kg and, >1000kg.

The ecological roles of predators within each network were calculated using four centrality metrics: (i) degree – a measure of the number of edges a node has with other nodes; (ii) betweenness – the number of times a species is between a pair of other nodes; (iii) closeness – how close a node is to all other nodes, considering the entire network and; (iv) eigenvector – the overall effects of each species on all of its partners simultaneously. We calculated these measures using the '*igraph*' package. These are measures of centrality recommended in Delmas et al.[28] These measures of centrality are commonly used to assess the trophic positioning and influence on a network. For example, such node-level measures have been used to assess the role of species in marine food webs,[75,76] salt marshes[76,77] and, paleoecological food webs.[78] We also calculated the mean prey body mass, number of predators and numbers of resources and consumers in food webs. We then synthesized changes in the ecological roles of predators in the Late Pleistocene and current-day food webs using a principal component analyses with the '*prcomp*' function. All data and original code are available at Zenodo (https://zenodo.org/records/13755842).